



Wasp sex ratios when females on a patch are related

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Optimality theory of sex allocation in structured populations has proved remarkably successful in explaining patterns of facultative sex ratio behaviour in numerous species. Extensions to the basic theory have included more specific aspects of species biology, including the relatedness of interacting individuals. We considered the sex ratio decisions made by female *Nasonia vitripennis* wasps when they were ovipositing on a patch with either relatives or nonrelatives. Theory predicts that females should produce more female-biased sex ratios when ovipositing with relatives, for example sisters, than with unrelated females. This is because related females should limit the level of local mate competition between their sons for female partners. Contrary to theory, two experiments showed that female sex ratio behaviour was unaffected by the relatedness of their oviposition partner, and was also unrelated to an environmental cue that could signal relatedness, i.e. whether females responded differently to sisters emerging from the same or a different host. Instead, in both experiments, we found that only wasp strain significantly influenced sex ratio. A meta-analysis of studies conducted on a range of species on the effects of the relatedness of oviposition partners on sex ratio failed to show the predicted pattern. We discuss why females appear to behave in a maladaptive way when allocating sex under these conditions, and suggest that weak selection and/or conflict between females over optimal sex ratios may influence the evolution of kin discrimination.

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The study of female sex ratio behaviour when populations are structured has proved to be one of the most productive and successful areas of behavioural ecology (Godfray 1994). Hamilton (1967) was the first to show that, if mating takes place between the offspring of N mothers, and then only the daughters disperse, the unbeatable or evolutionarily stable sex ratio (proportion of males, r) is given by $r = (N - 1)/2N$. Therefore, when N is small, so that few females contribute eggs to a patch, a female-biased sex ratio is predicted. Hamilton (1967) described this mechanism leading to a female-biased sex ratio as local mate competition (LMC). The female bias can be explained in a number of equally valid ways (Frank 1986a, 1998), but a useful conceptualization is that it decreases local competition between related males (brothers) for mates, and it provides more females with which sons can mate (Taylor 1981). There is huge empirical support for

LMC across a range of species, showing variation in overall sex ratios consistent with Hamilton's prediction, as well as facultative adjustment of offspring sex ratios by individuals in response to variation in N (e.g. Charnov 1982; Hardy 2002).

Since Hamilton's original paper, LMC theory has been extended in numerous directions incorporating different aspects of behaviour and ecology that may be important for particular organisms (Godfray 1994; Hardy 1994; Frank 1998). This body of theory offers enormous potential for more quantitative tests of LMC theory, which could explain variation in offspring sex ratios that is currently not well understood. Furthermore, and more generally, the close fit between theory and data that can be expected with sex ratios provides an excellent opportunity for examining the degree of precision with which natural selection shapes behaviour (Herre 1987; West et al. 2000). However, there is a severe lack of empirical work testing these extensions of LMC theory. We are conducting a long-term project testing the predictions of extended LMC theory models in the parasitoid wasp, *Nasonia vitripennis*. This is the ideal organism for such research, because we know that basic LMC theory applies to this species, and

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that females facultatively alter their offspring sex ratios with respect to the estimated level of LMC; however, there is also much unexplained variation in the sex ratios produced by females (Werren 1980, 1983; Orzack et al. 1991; Molbo & Parker 1996).

In this study, we were concerned with the predictions of models that allow the females laying eggs on a patch to be related (Frank 1985, 1986b, 1998; Bulmer 1986; Taylor & Crespi 1994; Courteau & Lessard 2000). In this case, theory predicts that, for a given number of females per patch (N), if females can assess their relatedness to other females laying eggs on a patch, then they should produce more female-biased sex ratios when they share a patch with relatives than with nonrelatives (Frank 1985, 1998; Taylor & Crespi 1994). This prediction arises because, when a female is related to the males produced by the other females on the patch, then she is also selected to decrease the competition that these males will encounter (i.e. reduce the level of LMC). Our first aim was to test this simple prediction with two experiments on *N. vitripennis*. In our experiments, females oviposited with either a sister or an unrelated female. Females could potentially assess relatedness through direct (genetic) or indirect (environmental) cues (Grafen 1990; Ode et al. 1995). We then also manipulated an environmental cue, testing whether females responded differently to sisters emerging from the same host, with shared environmental olfactory cues, than to sisters emerging from a different host. Our second aim was to assess the empirical literature testing this prediction more generally. We did this with a meta-analysis (Rosenthal 1991) and a consideration of previous experimental designs. This approach allowed us to determine the existence and magnitude of any overall pattern hidden among individual studies.

METHODS

Study Organism

Nasonia vitripennis (Hymenoptera: Chalcidoidea) is a gregarious parasitoid wasp of dipteran pupae, including numerous species of Calliphoridae and Sarcophagidae. Females typically mate once before dispersing to find new oviposition sites. Males have small wings and are unable to fly, remaining at the site of adult emergence to compete with each other for matings with emerging females. Females lay clutches of 20–40 eggs and limit oviposition in previously parasitized hosts (superparasitism) if possible. Since *N. vitripennis* is haplodiploid, the sex ratio can be facultatively altered by females choosing whether or not to fertilize an egg (producing diploid females or haploid males, respectively). We conducted two experiments, in which we used wasps from two strains recently collected from the field (HV236 and HV307, collected in summer 2002 from bird boxes in Hoge Veluwe, Netherlands, by L. W. Beukeboom; each strain was initiated from the wasps emerging from a single nest). For the second experiment, we also used the laboratory red-eye mutant marker strain STDR. All wasps were maintained before the experiment in mass culture, with *Calliphora vomitoria* pupae as hosts, at

25°C, in a 16:8 h light:dark photoperiod. Under these conditions, males emerge after 13 or 14 days, with females emerging soon afterwards.

Experiments

Experiment 1

Mated females from the two field strains were isolated and given three fresh hosts on which to oviposit. After oviposition, each host was placed in a separate glass vial with a cottonwool plug. The offspring were allowed to emerge and mate (with a sibling) for 48 h, and then individual mated females were allocated at random to one of the three experimental treatments: (A) two females from the same host together; (B) two females from the same mother but from different hosts together; (C) two females from the different strains (also from different hosts). Treatments A and B were repeated for both HV236 and HV307. To avoid pseudoreplication, each mother provided offspring for only one replicate. After being placed together in pairs in glass vials, females were pretreated with access to a fresh host for 24 h followed by access to honey solution for another 24 h. This procedure allows females time to obtain protein via host feeding and mature eggs. After the pretreatment, each pair of females received six fresh hosts for another 48 h to test the sex ratio behaviour of females when ovipositing with either a sister or an unrelated female. After 60 min, a one-way escape tube, made from a cut-to-size 1-ml pipette tip, was put on the vials to allow females to disperse after oviposition if they wished (to limit the level of superparasitism: Werren 1983; Godfray 1994). After 48 h, all females were removed and the hosts were incubated at 25°C. Offspring were allowed to emerge and die, and then the number and sex of all offspring were recorded. We analysed broods from 341 pairs of females, and the sample sizes for the three treatments ranged from 64 to 72.

Experiment 2

Identical methods were used for experiment 2, except that to produce the experimental females, the mother received two hosts instead of three to parasitize, before being placed in separate glass vials. For treatment C, the unrelated females were STDR red-eye marker females rather than the alternative field strain. This allowed us to follow the sex ratio behaviour of individual wasps. STDR females were reared in the same way as the field strains, and one female was randomly chosen and placed with a female from either HV236 or HV307 before the pretreatment and sex ratio testing as above. After emergence of the offspring, the offspring were genotyped by eye colour (wild-type black eyes indicated HV236 or HV307) and counted as before. We analysed broods from 262 pairs, and sample sizes ranged from 33 to 50 for each treatment.

Statistical Analysis

We defined sex ratio as the proportion of male offspring. For the analyses, the unit of replication was the patch or

female pair. Sex ratios were therefore based on the combination of two females' broods, except for treatment C in experiment 2, where offspring of the wild-type female could be identified from those of the STDR cofoundress.

Sex ratio data are characterized by binomially distributed data and are best analysed using generalized linear models, with binomial error structures and logit link functions (Crawley 2002; Wilson & Hardy 2002). However, problems in significance testing can arise if the data are overdispersed; dispersion is measured by calculating the so-called dispersion parameter from the residual deviance and residual degrees of freedom following model fitting (Crawley 2002). The data from both experiments were somewhat overdispersed (dispersion parameters > 4 in both cases). The analyses presented below are therefore based on the use of general linear models using arcsine-transformed sex ratios. Model simplification was carried out (Crawley 2002) to test the significance of main effects and interactions. Differences between treatment levels were tested by collapsing levels together and analysing whether there was a significant change in the variance explained by the model. If there was not, model simplification proceeded. A separate analysis was also undertaken using generalized linear models with the appropriate binomial errors and link function. Although not presented here, this analysis confirms the patterns presented below. Means are presented \pm SE.

Meta-analysis

This methodology takes a standard measure of the magnitude of the statistical effect from each study, hereafter effect size, and uses it as the response variable in a comparative analysis. The effect size used is r , the correlation coefficient, which varies between 1.0 and -1.0 . In the case examined here, we used the correlation coefficient of the relation between the offspring sex ratio and the relatedness of females laying eggs on a patch. The effect size would be positive if the sex ratio shift followed the predicted pattern (laying a more female-biased sex ratio when with closer relatives) and negative if it were in the other direction. Larger positive values of r represent a more precise positive correlation between the offspring sex ratio and relatedness of females laying eggs on a patch, and the value of r^2 represents the proportion of variance in the offspring sex ratio that can be explained by variation in relatedness.

We found studies from which to obtain relevant data by performing literature searches using the ISI Web of Science, forward and backwards searching through the citations of all the papers on our list and other key references and as part of a literature survey when writing a book chapter. Effect sizes were calculated using standard methodology (Rosenthal 1991; Rosenberg et al. 2000). Briefly, in some studies, the effect size is given as the Pearson correlation coefficient (r), the percentage of variance explained (r^2) or the Spearman rank correlation coefficient (r_s); in other cases, the effect size can be calculated from a test statistic (e.g. t , F , χ^2 or P value) and the sample size. The formulas for calculating r from test statistics are given in standard meta-analysis texts (Rosenthal 1991)

and are also implemented in the statistical calculator of the package MetaWin 2.0. (Rosenberg et al. 2000).

RESULTS

Experiment 1

Within each strain, there was no significant difference between treatments A and B (general linear models following model simplification, HV236: $F_{1,206} = 2.94$, $P = 0.09$; HV307: $F_{1,195} = 0.54$, $P = 0.47$; Fig. 1). A power analysis showed that the minimum significant difference between individual treatment levels that we could resolve as significant was 0.03 or less ($\alpha = 0.05$, power = 0.8). Females therefore did not differ in the sex ratio produced when they oviposited with a sister from either the same or a different host. There was a highly significant difference between the two strains across treatments A and B (mean sex ratio across treatments A and B, HV236: 0.316 ± 0.003 , HV307: 0.205 ± 0.003 ; $F_{1,273} = 50.82$, $P < 0.0001$; Fig. 1). This difference between lines made interpretation of the effect of treatment C more difficult than expected. The mean sex ratio of females ovipositing with unrelated females was intermediate to the sex ratios produced by HV236 and HV307 females that laid with sisters (Fig. 1). If females produce a lower sex ratio when ovipositing with kin than when ovipositing with unrelated females, as predicted, then females in treatment C should have produced a higher sex ratio than those in both strains across the combined treatments A and B. However, there was no significant difference in sex ratio across treatment ($F_{1,339} = 2.60$, $P = 0.11$).

Experiment 2

Fitting a general linear model with treatment and strain as independent variables, there was no significant effect of treatment ($F_{2,258} = 1.34$, $P = 0.26$; Fig. 2) and no

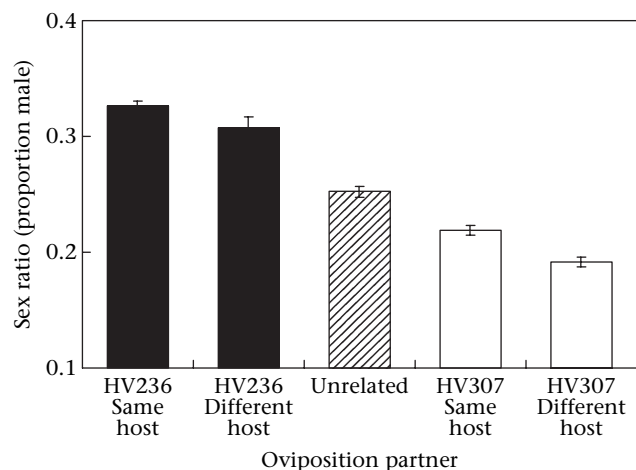


Figure 1. Female sex ratio behaviour and oviposition partner (experiment 1). Females were either with a female from the same strain (■: HV236; □: HV307) or were unrelated (▨: one HV236 female with one HV307 female). Error bars show binomial standard errors.

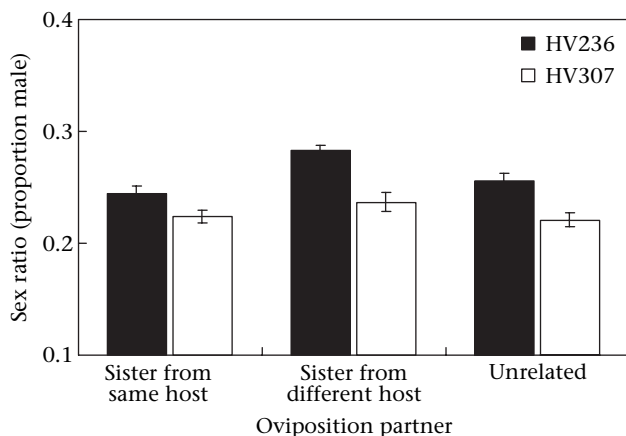


Figure 2. Female sex ratio behaviour and oviposition partner (experiment 2). Error bars show binomial standard errors.

significant interaction between treatment and strain ($F_{2,256} = 0.32$, $P = 0.73$). The minimum significant difference between individual treatment levels that we could resolve as significant was 0.03 or less ($\alpha = 0.05$, power = 0.8). There was a highly significant effect of strain on sex ratio, however (mean sex ratio, HV236 females: 0.267 ± 0.004 , HV307 females: 0.229 ± 0.003 ; $F_{1,260} = 7.89$, $P = 0.005$).

Meta-analysis

Including our work, there have been seven tests in five species of the prediction that increased relatedness between females laying eggs on a patch should lead to a more female-biased sex ratio (Table 1). These studies show no consistent trend towards more female-biased sex ratios when females laying eggs are related (mean effect size: -0.056 , 95% CI: -0.079 to 0.113 , $P > 0.23$; Fig. 3).

DISCUSSION

Theory predicts that when a female lays eggs on a patch under conditions of LMC, she should produce a relatively more female-biased sex ratio if she is related to the other females laying eggs on that patch. However, in contrast to

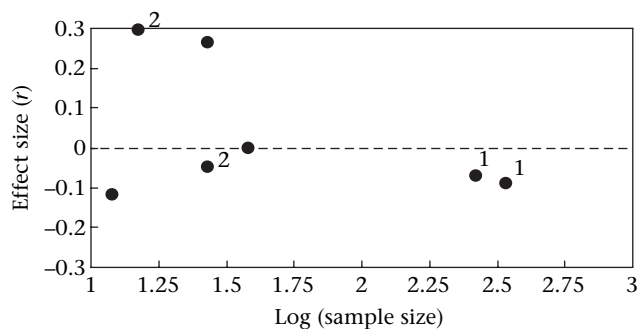


Figure 3. The effect size (r) of the relation between offspring sex ratio and relatedness of females laying eggs on a patch, plotted with respect to log (sample size). A positive effect size (r) corresponds to a more female-biased sex ratio when females on a patch were more related, as predicted by theory. 1: This study; 2: Taylor & Crespi 1994; see also Table 1.

this prediction, we found in the parasitoid wasp, *N. vitripennis* that the offspring sex ratio was not adjusted in response to (1) whether the other female laying eggs on a patch was a sister or nonrelative, or (2) an environmental cue that may suggest whether the other female laying eggs on the patch is a relative (developed in same host) or not (developed in a different host); (Figs 1, 2). Our results did show a significant effect of wasp strain on sex ratio, indicative of genetic variation in sex allocation in *N. vitripennis*, as has been reported (Orzack et al. 1991). Each strain was derived from wasps from a different bird's nest, and presumably any genetic differences represent segregating variation in sex ratio in the Hoge Veluwe population as a whole.

Why do our results not support the predictions of theory? One possible explanation is that females cannot assess their relatedness to the other females on a patch. This hypothesis is consistent with our previous result in *N. vitripennis* concerning kin discrimination of mating partners (Reece et al. 2004; Shuker et al. 2004), as well as the general lack of kin recognition in social and nonsocial insects (Keller 1997; Fellowes 1998; Sundström et al. 2003). An alternative possible explanation is that related females rarely lay eggs on the same patch, and so there has been limited selection for kin discrimination and the

Table 1. Studies of how sex ratio varied with relatedness between females on a patch, from which data for meta-analysis were extracted

Species	Study	Calculation of effect size	Effect size (r)	N
<i>Cardiocondyla obscurior</i>	Cremer & Heinze 2002	Used raw data in figure 1 to get $t_{10} = 0.376$	-0.1182	12
<i>Hoplothrips pedicularius</i>	Taylor & Crespi 1994	Two females per patch, $t_{25} = 0.23$	-0.046	27
<i>Hoplothrips pedicularius</i>	Taylor & Crespi 1994	Four females per patch, $t_{13} = 1.12$	0.2966	15
<i>Nasonia vitripennis</i>	This study	Experiment 1, $F_{1,339} = 2.60$	-0.0872	341
<i>Nasonia vitripennis</i>	This study	Experiment 2, $F_{2,258} = 1.34$	-0.0691	262
<i>Pegoscopus assuetus</i>	Frank 1985	Median same across treatments	0	38
<i>Tetranychus urticae</i>	Roeder et al. 1996	Reconstructed data in figure 1 to give $t_{25} = 1.374$	0.265	27

relevant sex ratio adjustment (Herre 1987). Within small patches of naturally occurring hosts, for instance around small vertebrate carcasses (including dead hatchlings in bird's nests), it may be unlikely that hosts would be available for emerging wasps to parasitize. Females would therefore have to disperse to find suitable hosts. Unless these hosts were easily found nearby, we might expect dispersing sisters to co-occur rarely on new patches. However, on large carcasses or around areas of continuous resources (e.g. waste dumps: Werren 1983), hosts may be available for emerging females to parasitize close by, and the probability of sisters ovipositing together on patches may increase. We plan to test these possibilities by genotyping the wasps emerging from different kinds of patches in natural populations (e.g. Molbo & Parker 1996), and using these results to infer the relatedness of their mothers.

We also carried out a meta-analysis to determine the overall pattern across all studies in which the prediction that related females laying eggs on a patch will produce relatively more female-biased sex ratios had been tested. These studies, which included seven experiments on five species (Table 1), allowed us to evaluate the possibility that there is a consistent shift in the predicted direction, but that this shift is generally too weak to be detected with the samples sizes used. We found no support for this prediction; overall, there was no consistent trend to lay a more female-biased sex ratio when the other females on a patch are relatives (Fig. 3). The only study that showed a significant effect of relatedness between females on the offspring sex ratio is that of Roeder et al. (1996), with the spider mite *Tetranychus urticae*. However, the importance of this result is not clear because of possible problems with Roeder et al.'s experimental design and data analysis. Specifically, their experimental design confounded relatedness between females on a patch with relatedness to their mates, which can also favour a sex ratio shift in the same direction (Reece et al. 2004). Furthermore, their data analysis involved a comparison across treatments where differences in the sex ratio could be explained by other factors, such as between-line differences in the sex ratio. When we used Roeder et al.'s figure to reconstruct the data from the two appropriate treatments (females from their OP1 population ovipositing with siblings or nonsiblings), we found no significant difference in the sex ratio ($P > 0.10$; Table 1).

To conclude, why is there no general pattern for sex ratio shifts in response to relatedness? One possibility, as discussed above, is that related females rarely lay eggs on the same patch and so there is a lack of selection for such shifts (Herre 1987; Herre et al. 1997; West & Herre 1998). While this seems likely in species such as fig wasps (Nason et al. 1998), it is less likely in species such as the ants, mites and thrips that have been studied (Table 1). A more general reason why sex ratio shifts in response to relatedness may not evolve is conflict between females on a patch. Specifically, it can be in a female's interest to deceive the other females on a patch about her relatedness, making kin recognition and subsequent sex ratio adjustment unstable. For example, consider a focal female when two unrelated females lay eggs on a patch, and when sex ratio is adjusted in response to relatedness

as predicted by theory. The fitness of the focal female would be greater if the other female lays a more female-biased sex ratio, because it would increase the mating success of her sons (Hamilton 1967). However, because the females are unrelated, the other female will do the opposite (lay a less female-biased sex ratio), so the focal female is selected to deceive the other female about her relatedness. The best tactic for the focal female is to signal to the other female that they are relatives, so that the other female produces offspring with a more female-biased sex ratio. However, when the two females laying eggs on a patch are related, the inclusive fitness of the focal female is maximized when they both produce a more female-biased sex ratio (Frank 1985, 1998; Taylor & Crespi 1994), so she again wants to signal that she is a relative. Consequently, all females always want to signal to the other females on the patch that they are relatives. Modelling has shown that, in an analogous situation with social insects, this selects against kin recognition (Reeve 1998). Therefore, we might expect shifts in sex ratio behaviour only when some estimate of relatedness is uncheatable, such as when individuals must assess merely whether they are native to a patch or an immigrant (Taylor & Crespi 1994).

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